Growth variability of two native pine species on Corsica as a function of elevation

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ABSTRACT

Located in the western Mediterranean basin, the island of Corsica (France) is expected to be strongly affected by climate change. With its diverse topography and altitudinal gradients from sea level to 2700 m asl, it hosts two pine species, i.e. *Pinus pinaster* in lower areas and *P. nigra* ssp. *laricio* in higher regions up to the upper tree line. However, the growth performance of these two dominant forest tree species along different elevation belts is still unknown, so it is not clear how climate change will affect their distribution. The relationships between tree age, elevation, and growth performance were evaluated using growth trajectories derived from tree-ring analysis of pines in different age classes at 13 sites across the island, ranging from sea level to 1600 m asl. Results show that the growth performance of both species under the same environmental conditions is very similar. For both species, we found that growth rates change over time, whereby trees younger than 50 years grew faster than older trees. We also found that *P. pinaster* is becoming common at higher elevation sites, indicating a migration upslope.

1. Introduction

The Mediterranean region is expected to be strongly impacted by increasing drought stress during the summer months due to rising temperatures and decreasing annual precipitation (Giorgi, 2006; Gao and Giorgi, 2008; Hertig et al., 2013; IPCC, 2017). This will particularly influence the distribution and productivity of forest ecosystems and thus forest management (Ruiz-Labourdette et al., 2012; Reyer et al., 2014). For this reason, it is important to understand the growth behavior of affected tree species throughout their distribution ranges. Some islands in the Mediterranean Sea exhibit a complex topography that yields varying ecological conditions, from coastal areas with typically Mediterranean climates, i.e. dry summers and wet winters, up to alpine regions with continuous snow cover in winter and multiple frost days. Vegetation zones containing a variety of tree species form along elevation gradients. Each species has its own way of dealing with the climatic conditions of the Mediterranean region as well as a different potential to adapt to climate changes. *Pinus* species are widespread in the study area and constitute important timber species. In order to appropriately adjust silvicultural management strategies, it is important to know how different species of this genus will cope with the predicted climatic changes at different elevations.

The French island of Corsica, located in the western Mediterranean basin, is characterized by strong elevation gradients over short distances. The island is still largely forested and is an exceptional study area because of its two native pine species: *Pinus pinaster* (Maritime Pine) and *Pinus nigra* ssp. *laricio* (Corsican Black Pine, herein referred to as *P. nigra*). The former is mostly distributed at lower elevations, whereas the latter populates higher regions up to the upper tree limit. The distribution ranges of the two species overlap in a broad elevation band ranging from ca. 600–1300 m a.s.l. Due to the long settlement history in the Mediterranean basin, the regional ecosystems are far from being natural. Long-term deforestation at lower elevations (Barbet-Massin and Jiguet, 2011) and frequent natural and man-made forest fires have long shaped the landscape of Corsica (Pausas et al., 2008). However, the old-growth *P. nigra* forests at the upper timberline can be regarded as remnants of the natural forest in the Corsican Mountains. The distribution of the species has declined significantly as a result of the clearing of forests for pastures and orchards, especially at lower elevations. These anthropogenic activities have reduced and shifted the species realized niche to higher elevations (Barbet-Massin and Jiguet, 2011). At lower elevations, old-growth *P. nigra* stands have been

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replaced by younger forests consisting of mixed stands of *P. nigra* and *P. pinaster,* which are used commercially. It is therefore difficult to describe the natural distribution ranges of these two native pine species.

Both species have already been used successfully in dendroecological studies. For instance, Vieira et al. (2009) studied how growth response to climate and intra-annual density fluctuations of *P. pinaster* change with age. Studies by Hetzer et al. (2014) and Szymczak et al. (2014) present climate-dependent growth variations for *P. nigra* over long periods of time at high mountain sites on Corsica.

A commonly used parameter in dendroecological studies is the aspect of individual growth–ontogeny. Cumulative growth has been examined in a wide range of studies with different purposes. For example, Abiyu et al. (2018) used it to understand long-term human-environment interactions, Bräuning et al. (2013) reconstructed historical environmental development and Seo et al. (2018) used it to analyze silvicultural treatments. This measure has also proven useful for comparing growth variations of different species (Brienen and Zuidema, 2006; Black et al., 2008; Bigler and Veblen, 2009) and along elevation gradients (Di Filippo et al., 2017). Growth trajectories are an established means of analyzing individual long-term tree growth and investigating differences in growth performance between different tree populations. They show age-diameter relationships as cumulative growth curves.

The aim of this study is to shed light on the growth characteristics of *P. nigra* and *P. pinaster* on the island of Corsica in relation to elevation and age. For this purpose, we sampled 239 trees of different age classes at thirteen sites located along an elevation transect. Tree-ring analysis was conducted to: (i) compare the growth of the pine species in the altitudinal belt in which they co-occur, (ii), test if growth performance changed over time in different age classes and (iii) evaluate species-specific growth performance in different altitudinal belts.

2. Material and methods

2.1. Study area

With a spatial extent of 8680 km^2, the mountainous island of Corsica is the fourth largest island in the Mediterranean Sea. It is characterized by steep elevation gradients over short distances. The highest mountain, Monte Cinto, is located ca. 30 km north of the study transect and peaks at 2706 m asl. We selected thirteen pine stands located along a 60 km east-west transect crossing the central mountain range (Fig. 1). The two studied pine species, *P. nigra* and *P. pinaster*, are widespread in the Mediterranean basin. *Pinus nigra* occurs naturally at an elevation range of approximately 700–1800 m asl, whereas *P. pinaster* appears at 600–1300 m asl (ONF, 2006). However, *P. pinaster* is also able to inhabit lower elevations, even down to sea level (Wahid et al., 2006). This results in different spatial distribution patterns, with *P. pinaster* dominating in the lowlands and *P. nigra* at higher elevations. However, there is a transitional belt in which both species coexist.

Study sites were selected to achieve a regular vertical distance between sites along an E–W transect, as well as homogenous age distribution among sites. This was especially difficult at low elevations because forested areas in the lowlands of Corsica are dominated by *Quercus pubescens*, *Quercus ilex* and *Castanea sativa* (Gamisans, 1991). Six of the thirteen selected study sites contain only *P. pinaster* and four sites contain only *P. nigra*. Additionally, there are three sites at which both species occur. The stands on the sites were selected with average tree coverage below 30%. Most stands were comprised solely of pine trees, but the three highest sites were characterized by mixed stands of *P. nigra* and *Fagus sylvatica*. Due to the dominance of granites and metamorphic rocks on the island, the soils at all study sites were acidic.

According to the Köppen-Geiger classification, Corsica is characterized by temperate climate with a dry summer (Peel et al., 2007). The elevation gradient is reflected in the island's spatial climatic variability, as depicted by climate diagrams from different elevation

belts (Fig. 1). Climate station coverage in this mountainous region is sparse. The Evisa station is the highest available station on Corsica. The Ajaccio station represents the coastal sites. The climate at Ajaccio is typically Mediterranean, with very little precipitation and high temperatures in summer (e.g., 6.6 mm rainfall and a mean monthly temperature of 22.8 °C in July). The majority of precipitation at both sites occurs in winter and autumn, but the mean annual precipitation at Evisa is more than twice than at Ajaccio, and the annual mean temperature is 5.1 °C lower (Météo France, 2018).

2.2. Tree-ring analysis

We used cumulative growth curves to evaluate the growth performance of the two pine species in different environmental conditions across the island. A total of 239 living trees were sampled at thirteen sites across the island between April 2017 and January 2018. Two increment cores were taken at breast height from opposite sides of each tree. Trees were cored perpendicular to the slope to avoid the possible influence of reaction wood. Samples were prepared using sand papers of decreasing grain size to enhance visibility of the rings (Speer, 2012). Tree-ring widths were measured to an accuracy of 0.01 mm using a LINTAB 5 System (RINNTECH, Heidelberg, Germany). The cores were dated, then cross-dated visually and with statistical tests (sign test, *t*-test) performed in TSAPWin 4.7 (Rinn, 2003). Cross-dating was confirmed by comparison with existing Corsican tree-ring width chronologies (Szymczak et al., 2014). Age-related growth trends were removed with the R-package dplR (Bunn et al., 2018) using a cubic smoothing spline that equals a frequency response of 50% at a wavelength depending on the respective series length (0.67 * series length in years). Climate-growth relationships were calculated with data obtained from five Météo France stations located as close as possible in horizontal and vertical distance to the tree sites. The climate records span the period 1978 to 2016. An age-diameter relationship was generated for each tree. If neither of the sampled cores included the pith, the curvature of the innermost rings was used to estimate the number of missing rings (Esper et al., 2008). The widths of the missing rings were estimated as the mean width of the last five visible rings (Xu et al., 2012). Diameter at breast height (DBH) below bark was calculated by summing the ring widths of the two opposing radii.

The examined individuals were divided into three age classes: younger than 50 years, between 50 and 100, and above 100 years of cambial age. These class age boundaries were selected following the definition of adult rings as those older than 50–100 years of cambial age (Esper et al., 2008). We therefore use the term "juvenile" for trees below the age of 50 years. By dividing the trees into age classes, we ensured sufficient and similar quantities of trees in each age class. Furthermore, the sites were grouped into low (10–750 m asl), middle (790–1240 m asl) and high (1400–1600 m asl) elevation belts, which were defined according to species distributions. The boundaries were selected in such a way that the middle elevation belt includes all sites in which the two pine species co-occur. Hence, the low elevation belt contains only *P. pinaster* and the high elevation belt only contains *P. nigra*. To enable the comparison of the growth performance of trees in different age classes, elevation belts, and within species, a diameter-at-breast-height (DBH) threshold was selected. The DBH threshold was set to 20 cm to include as many trees as possible and thus allow for a comparison. 91% actually reached or exceeded this diameter size by the time of sampling. We first compared cumulative growth at the sites where both species occur. Thereafter, growth variations related to differences in age and elevation were analyzed.

3. Results

3.1. Age distribution, tree-ring chronologies, and climate signals

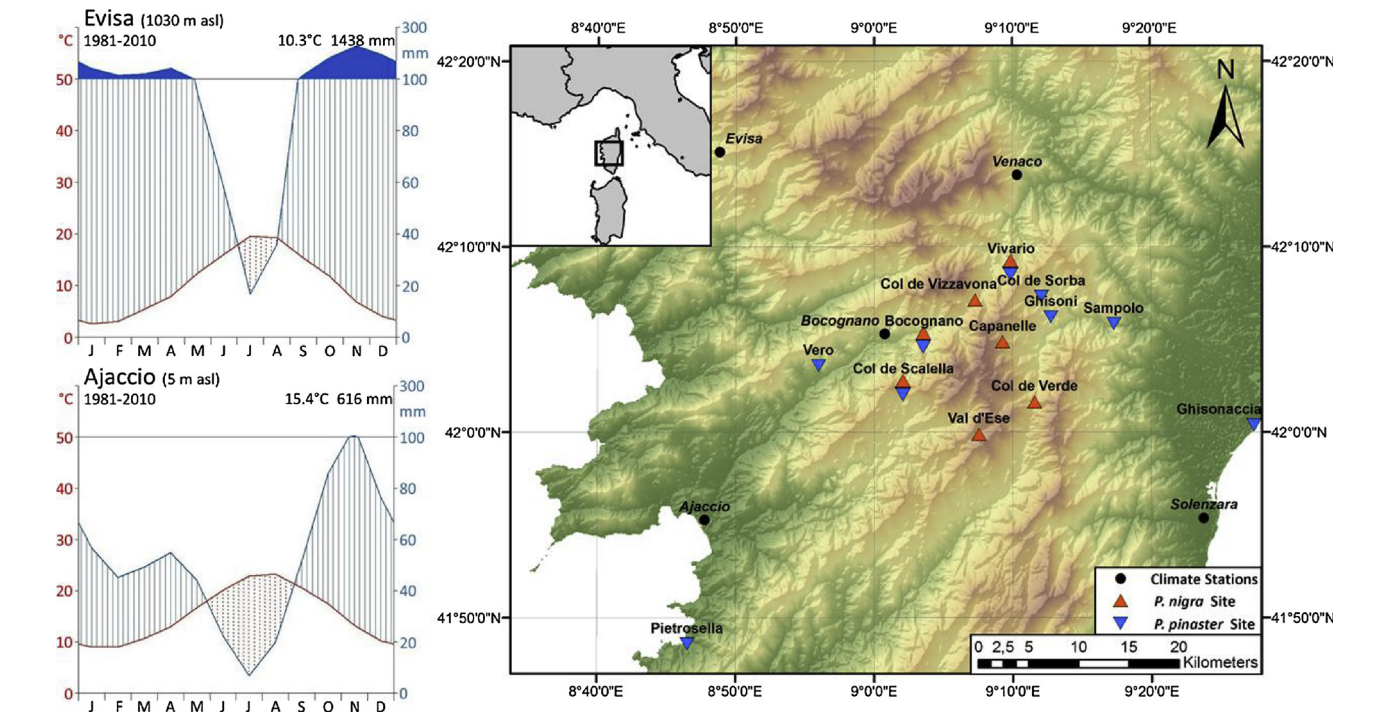Mean tree age and mean DBH were highly variable between the

Fig. 1. Climate characteristics of the study area based on Météo France data. Diagrams were created with the R-package climatol (Guijarro, 2018; R Core Team, 2018). Map showing the location of study sites and climate stations. Digital Elevation Model based on SRTM data (USGS, 2018).

Table 1
Characteristics of the study sites and occurring pine trees. *P. nigra*: n = 117, *P. pinaster*: n = 122. Dashed lines indicate elevation belts. Highlighted in grey are the sites in which the species co-occur. Rbar: mean interseries correlation. EPS: expressed population signal.

Site	Elevation [m asl]	Number of *Pinus nigra*	Number of *Pinus pinaster*	Mean age (Range) [yrs]	Estimated mean DBH ± SD [cm]	Chronology length sample depth > 5	Rbar	EPS
Capanelle (CA)	1600	17	-	169 (45-390)	41.2 ± 21.9	1742-2017	0.26	0.76
Val d'Ese (VA)	1560	17	-	27 (25-29)	25.9 ± 3.0	1991-2016	0.18	0.78
Col de Verde (VD)	1400	12	-	235 (176-410)	69.8 ± 16.2	1786-2017	0.50	0.87
Col de Scalella (CS)	1240	7	9	37 (18-71)	36.1 ± 10.2	1981-2017	0.46	0.89
Col de Vizzavona (CV)	1160	29	-	173 [60-368]	45.6 ± 18.3	1817-2017	0.46	0.93
Col de Sorba (SO)	1080	-	12	36 (31-39)	13.0 ± 4.1	1916-2017	0.44	0.92
Vivario (VI)	1000	24	12	98 (24-191)	34.2 ± 11.3	1842-2017	0.26	0.89
Bocognano (BO)	790	11	10	40 (25-54)	29.8 ± 6.8	1973-2016	0.55	0.95
Ghisoni (GH)	750	-	13	60 (50-75)	59.0 ± 9.3	1957-2016	0.67	0.96
Vero (VE)	495	-	14	88 (58-104)	54.3 ± 12.1	1928-2017	0.59	0.95
Sampolo (SA)	380	-	18	34 (14-80)	33.6 ± 10.4	1979-2016	0.52	0.89
Pietrosella (PS)	15	-	17	33 (15-42)	35.8 ± 9.9	1982-2017	0.62	0.96
Ghisonaccia (GI)	10	-	17	43 (10-67)	32.7 ± 8.8	1955-2016	0.52	0.92

thirteen sites (Table 1). The oldest trees found were *P. nigra* in the high elevation belt, with a maximum age of 410 years (site CA). In contrast, the oldest *P. pinaster* tree was only 104 years old (site VE). Two of the three sites in which both species occurred showed comparable age distribution between species, whereas *P. nigra* was noticeably older than *P. pinaster* at site VI. Most chronologies showed a mean interseries correlation (Rbar) of > 0.3 (except for sites CA, VA and VI). The generally applied expressed population signal (EPS) threshold of 0.85 (Wigley et al., 1984) is exceeded by all chronologies except for the two highest sites (CA and VA).

The five highest elevation sites exhibit positive correlations between winter (DJF) temperature and tree-ring width (Fig. 2). For spring (MAM), this holds true only for the two highest sites. Summer (JJA) temperature is negatively correlated with ring width at most sites along the elevation transect. Correlations with precipitation are highly variable in winter. Spring precipitation is positively correlated with tree-ring width at most sites in lower elevation belts, while we found negative correlations at the two highest sites. Almost all sites show high correlations with summer precipitation, while only the western coastal site (PS) shows positive correlations with precipitation in autumn (SON).

3.2. Growth performance at sites where both species occur

To evaluate if growth of the two studied pine species differs under similar environmental conditions, the three sites where both species occur were assessed separately (Fig. 2). At these sites (CS: 1240 m asl, VI: 1000 m asl, and BO: 790 m asl), both pine species are within their preferred altitudinal range (ONF, 2006). The number of trees per species and age classes varies widely, as shown in Fig. 2A–C. Most of the
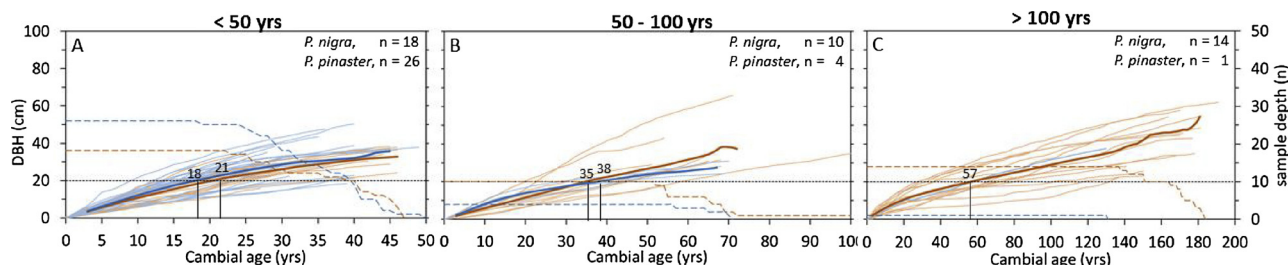
Fig. 2. Cumulative growth of *P. nigra* (orange) and *P. pinaster* (blue) at the sites where species occur (sites CS, VI, BO). Bold lines represent 7-year moving averages of mean growth trajectories per species (primary y-axis). Dotted horizontal lines indicate 20 cm DBH for reference. Dashed coloured lines indicate respective sample depth (secondary y-axis). Note differing x-axis scales for different age classes.

trees are younger than 50 years (60%), and 59% of those are *P. pinaster*. *Pinus nigra* is dominant in the two higher age classes. Only a single *P. pinaster* tree with a cambial age greater than 100 years was found. This indicates that the number of *P. pinaster* at higher elevations has increased, whereas the number of *P. nigra* has decreased at these sites during the past century.

To visualise the growth performance of each species, the average number of years needed to exceed a DBH of 20 cm is highlighted by vertical black bars in the Fig. 2A–C. In the juvenile tree age class (< 50 years of cambial age; Fig. 2A), *P. nigra* reached this threshold after 21 years and *P. pinaster* after 18 years. In the middle age class (50–100 years of cambial age; Fig. 2B), the threshold is reached after 35 and 38 years, respectively. The difference of only three years in both age classes suggests similar growth rates under identical environmental conditions. A species comparison cannot be conducted for the highest age class (> 100 years of cambial age; Fig. 2C) because only one *P. pinaster* was found in this category.

Pinus nigra underwent a considerable shift in growth performance between the three age classes: The trees in the highest age class took 57 years to pass the DBH threshold of 20 cm, while the trees in the middle age class required 35 years and the juvenile trees needed only 21 years. This implies an increase in juvenile growth rates by almost a factor of three. A comparable shift was also observed for *P. pinaster*, which reduced time to reach a stem diameter of 20 cm from 38 years in the middle age class to 18 years in the youngest age class.

3.3. Growth performance in different age classes and elevation belts

Classification by elevation resulted in 46 individuals of *P. nigra* in the high-elevation belt (Fig. 3A–C) and 71 individuals in the middle-elevation belt (Fig. 3D–F). The highest number of *P. nigra* trees was found in the category " > 100 years at 790–1280 m asl" (n = 42; Fig. 3F); the lowest number is in the category "50–100 years at 1400–1600 m asl" (n = 6; Fig. 3A). There are 43 *P. pinaster* in the middle-elevation belt (Fig. 3D–F) and 79 *P. pinaster* in the low-elevation belt (Fig. 3G–I). The distribution within the age and elevation categories, however, was highly variable. The majority of *P. pinaster* individuals are relatively evenly distributed in low age and elevation categories (Fig. 3D, G and H), while only eight of 122 sampled *P. pinaster* trees are situated in other categories (Fig. 3E, F and I).

Cumulative growth rates differed considerably between age classes and elevation belts. *Pinus nigra* in the young, middle, and oldest age classes needed 22, 53, and 39 years, respectively, to reach 20 cm DBH in the highest elevation belt. In the middle elevation belt, we found a more equally distributed change from 21 years (Fig. 3D) to 35 years (Fig. 3E) and 46 years (Fig. 3F). This implies that young trees grew faster to a DBH of 20 cm than old trees. The same trend was found for *P. pinaster* in its respective elevation bands, but with generally faster growth rates.

4. Discussion

4.1. Range of tree ages

Ideally, the preferred method for calculating growth trajectories includes sampling stands with homogenous age structures. However, this was not feasible in our heterogeneous study area. We sampled trees of different ages, ranging from 24 to 410 years (*P. nigra*) and 14 to 104 years (*P. pinaster*), respectively. However, since the trees were cored at breast height, the presented ages do not take into account the time needed to grow from sapling to sampling height (Bigler and Veblen, 2009). Therefore, our tree ages slightly underestimate cambial age. *Pinus nigra* is a long-lived species that can reach ages of more than 900 years, whereas the maximum age for *P. pinaster* is 200–300 years (Schütt et al., 2004; ONF, 2006). Since *P. nigra* trees at the upper age limit were found in single-species stands on Corsica (Szymczak et al., 2014), we assume that the combination of stressful site conditions and competitive pressure prevent trees from reaching ages well beyond 400 years. The oldest *P. pinaster* we sampled was only 104 years, well short of the species' potential maximum age. There are no extensive areas of *P. pinaster* forests in the lowlands along our study transect, and the existing stands do not host old growth individuals. We assume that this pioneer tree species is restricted to areas with a high frequency of disturbances, i.e. fires, slash-and-burn agriculture, and wind throw. Additionally, the life span of *P. pinaster* is reduced by pest infestation by the coccid *Matsucoccus feytaudi* which has eliminated around 30% of *P. pinaster* trees on Corsica since 2000 (UICN France, 2017).

4.2. Growth behaviour of both pine species under identical site conditions

A comparison of the two species growing under the same site conditions revealed no significant species difference between the cumulative growth of young (< 50 years) and middle-aged (50–100 years) trees. This result is in contrast to the report of UICN France (2017), which states that *P. nigra* is smaller in size than *P. pinaster* at a comparable growing stage. Two of the sites are located above 1000 m asl, an elevation where frost days are common (Rome and Giorgetti, 2007). We assume that these sites are at the upper distribution limit of *P. pinaster* on Corsica, where sub-optimal growth conditions result in lower growth rates.

4.3. Growth behaviour depending on tree age

Our results indicate that older trees needed more time to reach a DBH of 20 cm than younger trees. The only exception is the six *P. nigra* trees in the middle age class (Fig. 3B), but we interpret this result with great caution due to the low sample depth.

Climate-growth relationships derived from a tree-ring width network of *P. nigra* trees at the upper tree-line in the Corsican mountains indicate that tree-ring width is mainly influenced by summer (JJA) precipitation and, to a lesser extent, by February/March temperature (Szymczak et al., 2014). A combined summer temperature and
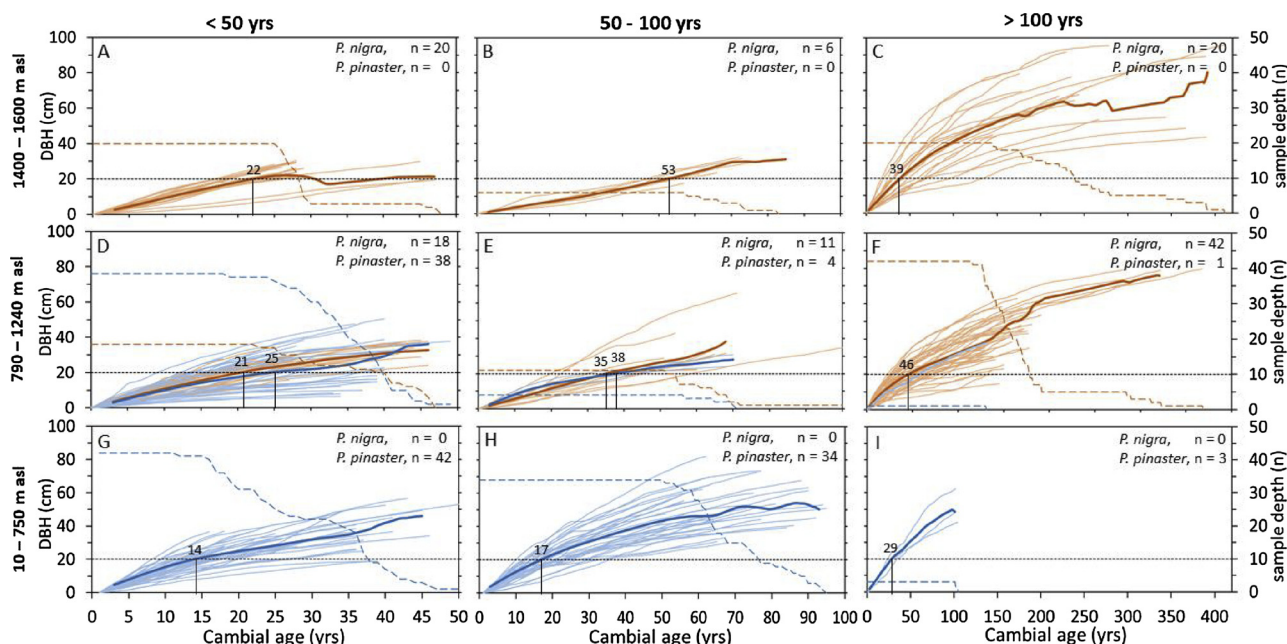
Fig. 3. Growth trajectories classified by tree age and elevation. *Pinus nigra* (orange), *P. pinaster* (blue). Graphs A–I contain different numbers of sites ranging from one (B, I) to four (D, E, G, H). Bold lines represent 7-year moving averages of mean growth trajectories per species (primary y-axis). Dotted horizontal lines indicate 20 cm DBH for reference. Dashed coloured lines display respective sample depth (secondary y-axis). Note the different x-axis scales for different age classes.

precipitation reconstruction based on $\delta^{13}C$ values and tree-ring width chronologies from *P. nigra* trees showed varying climate conditions over the last 600 years (Szymczak et al., 2014). During the juvenile phase of our oldest studied trees, the summer climate from ca. 1740 onwards can be characterized as cold-wet. This phase was followed by a warm-dry phase during 1920–1960, which corresponds roughly to the juvenile phase of the middle-aged trees in our study. The current climate phase, which started around 1960, can be classified as warm-wet and marks the climate conditions of the trees below 50 years of age. The slow growth of the middle-aged trees in the highest elevation belt can be attributed to the warm-dry climate conditions during their youth. A similar observation was made by Fyllas et al. (2017), who stated that water availability during May-August is the key determinant of tree growth across several tree species in mountainous forests in Greece, which have climatic conditions similar to those on Corsica.

Another factor that might have caused faster growth rates in recent years is the CO_2 fertilization effect. Kaushal et al. (1989) observed a 10% increase in diameter growth of *P. nigra* seedlings growing for one season at double CO_2 concentrations. However, Sánchez-Gómez et al. (2017) showed that elevated CO_2 can aggravate the effects of drought stress in *P. pinaster*. The influence of increased atmospheric CO_2 on tree growth remains uncertain (e.g. Brienen et al., 2017), particularly whether an initial positive response will be sustained over several years.

In the two other elevation belts, growth rates decreased with increasing tree age. These findings correspond with the observations of Bigler and Veblen (2009), who found a relationship between growth rate during the first 50 years of tree life and longevity. In general, slow-growing trees tend to have longer life spans than fast-growing trees (Abiyu et al., 2018). Fast-growing trees are more susceptible to disturbances because they invest less in defense strategies, have lower wood density and mechanical strength, and are less able to reduce growth during periods of stress (Bigler and Veblen, 2009). Since *P. pinaster* is a faster-growing species than *P. nigra*, this may also account for the different maximum ages of the two species.

4.4. Growth behaviour along the elevation gradient

Lower temperatures at higher elevations lead to shortened

vegetation periods and hence reduced ring widths (Oladi et al., 2011; King et al., 2013; Wang et al., 2015). This pattern is reflected in the ring widths of *P. pinaster*. However, the oldest age class of *P. nigra* does not follow this trend.

The climate-growth relationships (Table 2) indicate that tree-ring growth depends on both temperature and precipitation, although correlations with precipitation are generally higher. At high elevations, the persistence of the snow cover determines the beginning of the growing season. Growth in dry-warm summers is less vigorous than in humid-cool summers.

In contrast, winter climate conditions for sites in the low elevation belt are not as important, since it is usually not cold enough for snow-fall. The correlation patterns for the other seasons at low elevation show that tree rings are wider under cool-wet conditions than under dry-warm conditions; thus drought stress appears to be the limiting growth factor. Since summer drought is more pronounced in the low-lands, it can be expected that more drought-resistant species inhabit the drought-prone lower elevations. *P. pinaster* has a precipitation demand of at least 500 mm/yr (ONF, 2006), which is met even at sea level on Corsica (average precipitation is 616 mm/yr, cf. Fig. 1).

Our results imply that the two native pine species on Corsica have experienced changing regeneration dynamics over the past centuries. Given the dependence of tree growth on precipitation and the predicted increase in temperature and decrease in the annual number of precipitation days in the Mediterranean (IPCC, 2017), the altitudinal distribution of the two species may shift. As water becomes more limited at lower elevations and temperatures more favorable at higher elevations, both species may migrate upslope.

5. Conclusions

In this study, we developed growth trajectories of *P. nigra* and *P. pinaster* from a broad range of ages, elevations, and climate conditions. Results indicate that the two species perform similarly under the same conditions. However, we observed different growth performances depending on tree age and elevation along our transect. Trees younger than 50 years of cambial age grew faster than older trees when they were in a juvenile stage, especially in the low and middle elevation belt.

Table 2
Correlation coefficients (> +/−0.3) between tree-ring width chronologies and seasonal climate data. Positive correlations are highlighted in light grey, negative correlations in dark grey.

	Temperature					Precipitation			
	DJF	MAM	JJA	SON		DJF	MAM	JJA	SON
CA (1600 m asl)	0.47	0.33	-0.40				-0.32	0.54	
VA (1560 m asl)	0.45	0.53					-0.34		
VD (1400 m asl)	0.50		-0.34	-0.37				0.43	
CS (1240 m asl)	0.35		-0.39			-0.36		0.53	
CV (1160 m asl)	0.36		-0.40	-0.35				0.54	
SO (1080 m asl)		-0.36	-0.48			0.39	0.41	0.38	
VI (1000 m asl)			-0.49			-0.37	0.31	0.53	
BO (790 m asl)			-0.42					0.65	
GH (750 m asl)	0.54		-0.48			-0.41		0.45	
VE (495 m asl)			-0.38	-0.40				0.37	0.33
SA (380 m asl)		-0.36	-0.43	-0.36		0.36	0.43	0.54	
PS (15 m asl)	-0.34		-0.31				0.52	0.33	0.31
GI (10 m asl)		-0.42				0.41	0.35		

From the age distribution at the studied sites, a change in species frequency can be derived. A regeneration of *P. pinaster* in the middle elevation belt is apparent and may indicate that *P. pinaster* will supersede *P. nigra* in this elevation belt. This could pose serious implications for silvicultural activities because there is a much higher demand for *P. nigra* wood (personal communication with C. Panaiotis). *Pinus nigra* is also more water-demanding than *P. pinaster*; as water availability declines at lower elevations, the lower limit of the distribution range of *P. nigra* might move upward, further limiting the species' distribution. Ongoing analysis including dendrometer data and cambial phenology will provide growth models for different elevations (c.f. Gričar et al., 2014; Ziaco and Biondi, 2016), leading to more insight into the growth dynamics of the two species and their underlying forcing factors.

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